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Implicit Associative Learning Engages the Hippocampus and Interacts with Explicit Associative Learning

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Summary

The hippocampus is crucial for conscious, explicit memory, but whether it is also involved in nonconscious, implicit memory is uncertain. We investigated with functional magnetic resonance imaging whether implicit learning engages the hippocampus and interacts with subsequent explicit learning. The presentation of subliminal faces-written profession pairs for implicit learning was followed by the explicit learning of supraliminal pairs composed of the same faces combined with written professions semantically incongruous to those presented subliminally (experiment 1), semantically congruous professions (experiment 2), or identical professions (experiment 3). We found that implicit face-profession learning interacted with explicit face-profession learning in all experiments, impairing the explicit retrieval of the associations. Hippocampal activity increased during the subliminal presentation of face-profession pairs versus face-nonword pairs and correlated with the later impairment of explicit retrieval. These findings suggest that implicit semantic associative learning engages the hippocampus and influences explicit memory.

Introduction

Long-term memory has been subdivided into hippocampus-dependent memories, known as declarative or explicit memories, and hippocampus-independent memories, known as nondeclarative or implicit memories (Graf and Schacter, 1985; Squire, 1992a, Squire, 1992b; Squire and Zola-Morgan, 1991). While the formation and retrieval of declarative memories is associated with the conscious perception and retrieval of the learning material, nondeclarative memories are incidentally formed and reactivated without conscious awareness of retrieval. The distinction between hippocampus-dependent *conscious* memories and hippocampus-independent *nonconscious* memories is based on findings from patients with hippocampal damage. These patients exhibited deficits on tests of explicit memory in spite of a normal or near-normal performance on tests of implicit memory (Cohen and Squire, 1980; Corkin, 1968; Milner et al., 1968; Warrington and Weiskrantz, 1968). The anatomical dissociation between forms of implicit and explicit memory has also been supported by several functional neuroimaging studies in healthy human volunteers (for reviews, see Cabeza and Nyberg, 2000; Schacter and Buckner, 1998a). Together, many studies showed that the classic tests of implicit memory do not depend on the hippocampus. Yet, we hypothesize here that implicit tests may still engage the hippocampus if they require those cognitive computations that are tapped by explicit tests of memory.

For explicit memory, it is well established that the rapid formation and retrieval of new associations is mediated by the hippocampus and related cortices (Cohen and Eichenbaum, 1993; Henke et al., 1997, Henke et al., 1999; Mayes et al., 1998; Rolls and Treves, 1998; Sperling et al., 2001; Davachi et al., 2003). Doubts have been raised as to whether the rapid formation and retrieval of new associations were possible without conscious awareness (Bowers and Schacter, 1990; Schacter, 1998; McKone and Slee, 1997; Musen and Squire, 1993; Schacter and Buckner, 1998a; Squire, 1992a). Nevertheless, new functional neuroimaging studies in healthy volunteers (Henke et al., 2003a, Henke et al., 2003b; McIntosh et al., 2003; Rose et al., 2002; Schendan et al., 2003) and new behavioral findings in amnesic patients with hippocampal damage (Chun and Phelps, 1999; Curran, 1997; Rajaram and Coslett, 2000a; Rajaram and Coslett, 2000b; Savage et al., 2002; Yang et al., 2003) indicated that rapid associative learning and retrieval may indeed occur without conscious awareness and engage the hippocampus and parahippocampal gyrus. For example, Yang et al. (2003) examined priming for new word-word and color-word associations by use of a perceptual identification task in eighteen patients with lesions in the medial temporal lobe. In contrast to control subjects, and despite a normal level of single-item priming, these patients failed to show superior identification of old versus recombined word-word or color-word pairs. This finding is in line with the neuroimaging study (Henke et al., 2003b) that led us to the current experiments. In that study (Henke et al., 2003b), the hippocampus and perirhinal cortex were activated during the implicit encoding and retrieval of face-word pairs, and the degree of this activity correlated with the behavioral measure of the implicit associative retrieval. The nature of the implicitly formed associations remained unclear. While explicitly formed associations are often compositional and flexible and allow for generalization (Cohen and Eichenbaum, 1993; Dienes and Berry, 1997; Squire, 1992a), there is, as yet, little experimental evidence (e.g., Greene et al., 2001) for such representational qualities in implicitly formed associations.

Given the previous findings indicating that the hippocampus is involved in both implicit and explicit associative learning, we hypothesized that the two forms of learning would interact and that the hippocampus would be involved in this interaction. In three functional magnetic resonance imaging (fMRI) experiments, we

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investigated whether the implicit learning of twelve faces paired with written professions would influence the subsequent explicit learning of the same faces combined with either twelve identical or semantically congruous (to the subliminal pairs) or semantically incongruous written professions. We hypothesized that the effects of implicit learning on explicit learning would be facilitative or inhibitory, depending on whether the implicitly learned information was semantically congruous or incongruous with the explicitly learned information. Each fMRI experiment was conducted with a separate group of subjects.

To exclude the confounding effects of concurrent explicit stimulus processing on implicit stimulus processing, stimuli given for implicit learning were presented below the objectively defined awareness threshold (Cheesman and Merikle, 1984) with a visual backward masking paradigm (Henke et al., 2003b). Masking methods render stimuli invisible to the conscious mind by interrupting neural responses to masked stimuli (Kovacs et al., 1995; Rolls and Tovee, 1994). We refer to this presentation mode as "subliminal" and distinguish it from the "supraliminal" presentation mode, in which stimuli were presented for several seconds and without masks for conscious inspection and explicit learning. During presentations of masked stimuli, subjects were asked to engage in a visual detection task to ensure that they focused attention on the eye level of the subliminal faces. To this end, a fixation cross was briefly interjected between masks at a location which corresponded to the midpoint between the eyes of the subliminal faces at 1 sec intervals. The cross was sometimes replaced by a vertical or horizontal bar. The task was to indicate the occurrence of a bar.

Experiment 1 contained the semantically incongruous condition. Subliminal face-profession pairs were presented for the implicit processing of the faces and the written professions. Four different subliminal face-profession pairs were consecutively presented. Such a block of four subliminal face-profession pairs was immediately followed by the supraliminal presentation of the same four faces, given in the same order, for conscious learning (Figure 1A). These faces were now combined with new, semantically conflicting professions in comparison with those that had been presented for implicit learning. The delay between the presentation of a subliminal stimulus and its supraliminal counterpart was always 18 s. The experiment also included a neutral condition in which twelve subliminal faces were presented in combination with nonwords (e.g., bdfper). We chose nonwords because they do not contain meaning and hence exclude the implicit linking of word meanings to faces. The subliminal presentation of four face-nonword pairs was immediately followed by the supraliminal presentation of the same four faces with the first-time presentations of written professions, for conscious learning. Consequently, learning in the neutral condition remained uninfluenced by implicitly formed face-profession associations. The instructed strategy for explicit learning was to imagine the person presented acting in a scene typical of the written profession. This task automatically induces the semantic binding of the profession to the face. The experiment also included a subliminal and a supraliminal baseline condition, in both of which, contours of single heads without physiognomies were presented.

The designs of experiments 2 and 3 were identical to that of experiment 1, except for the nature of the subliminal professions used. The subliminal professions were congruous to the supraliminal professions in experiment 2 and identical with the supraliminal professions in experiment 3 (Figure 1A).

The retrieval part was exactly the same in all three fMRI experiments. The explicit retrieval of the explicitly learned face-profession associations was carried out 5 min after the completion of all learning trials. All explicitly learned faces were presented again, in a new order, as retrieval cues for the recall of the professions. The instruction was to remember the profession for each face and to indicate the superordinate category—academic or artist. This semantic translation ensured that *semantic* face-profession associations were being retrieved (Figure 1B).

In addition, we conducted a fourth, purely behavioral experiment in an additional subject group, using the same experimental procedure as in the three fMRI experiments. The aim was to test whether implicit learning would influence explicit learning if subliminal presentations consisted of written professions or nonwords alone. Therefore, we continued to present subliminal words and nonwords but replaced each subliminal face by a head contour without physiognomy (the same head contour was used in all trials; Figure 1A).

Results

Behavioral Data

Visual Detection Task

Accuracy (percentage correct) in detecting the flashed horizontal and vertical bars did not differ significantly between the three masked conditions in either of the experiments (ANOVA; for all, $p > 0.3$). Neither did the accuracy differ significantly among the four experiments with data pooled over masked conditions (ANOVA; $F_{(3, 51)} = 1.909$, $p = 0.14$; M/SEM % correct; experiment 1: 93.6/0.87; experiment 2: 93.5/1.3; experiment 3: 94.8/1.24; behavioral control experiment: 90.1/1.9).

Encoding

The instruction for the explicit learning of the face-profession pairs was to imagine the person presented acting in a scene of the indicated profession. In experiment 1 and in the behavioral control experiment, subjects were instructed to indicate by button press whether they were or were not able to imagine a scene for each face-profession pair. This instruction was changed in the subsequent experiments 2 and 3. Here, subjects were instructed to indicate by button press whether they found it easy or hard to imagine a scene for each face-profession pair. Consequently, behavioral measures of explicit encoding were the percentage of imagined scenes (experiment 1 and the behavioral control experiment) or the percentage of easily imagined scenes (experiments 2 and 3), as well as reaction latencies for these responses.

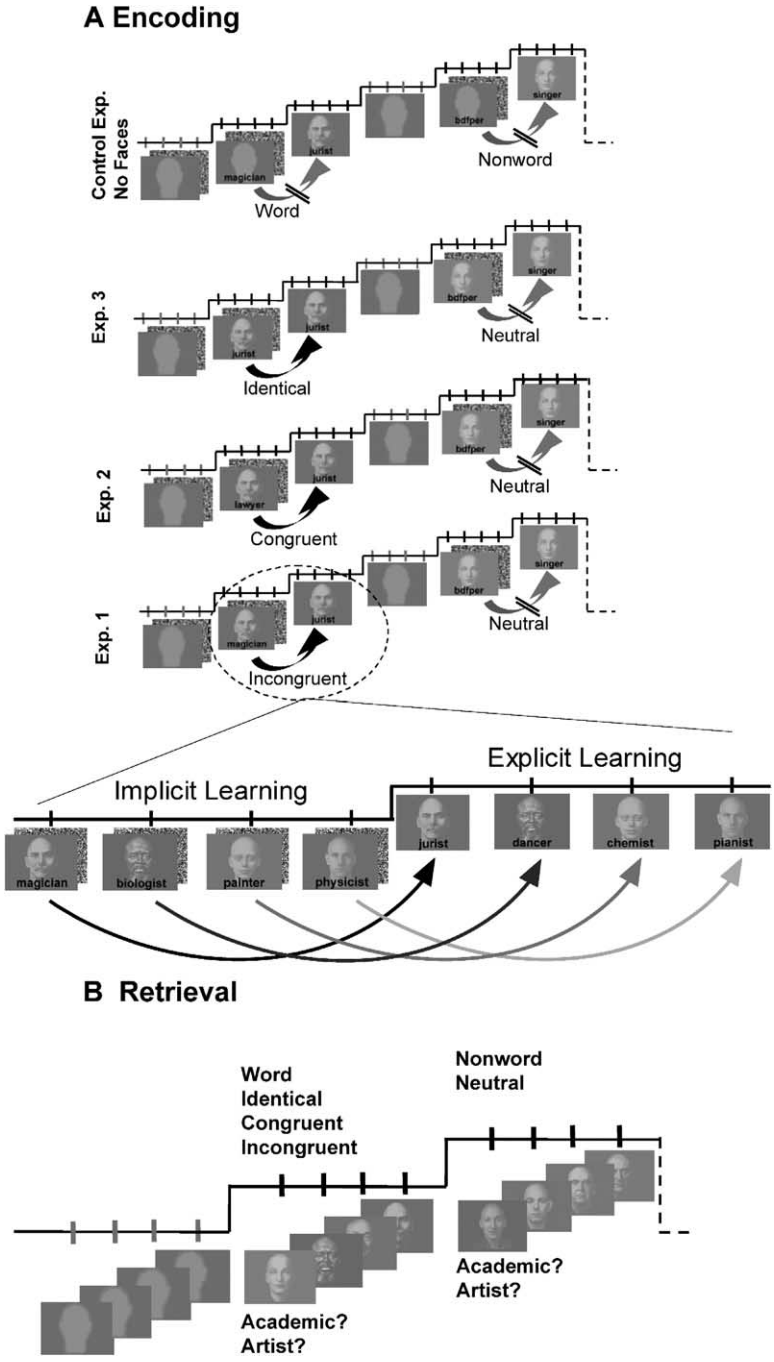

Figure 1. Experimental Design

(A) Encoding fMRI time series. Each condition is represented by one example stimulus. Masked conditions are indicated by one visual noise mask positioned behind the example stimulus. There were three blocks per condition (the figure illustrates only one task cycle).

(B) Retrieval fMRI time series. This time series contained the experimental retrieval condition, the neutral retrieval condition, and the baseline condition. Each condition is illustrated by one block of four stimuli. Subjects indicated by button press the professional category (academic or artist?) for each face. Faces used in Figures 1 and 2 were reproduced from the book *Heads* (1985) by permission of A. Kayser. Note that the original professions were written in German.

fMRI Experiments 1, 2, and 3

An ANOVA with the factors Condition (experimental versus neutral condition) and Experiment (denoting experiments 1, 2, or 3) and the dependent variable "percentage of (easily) imagined scenes" revealed no significant main effect for Condition but a significant interaction ($F_{(2, 40)} = 3.54$, $p = 0.038$; (three subjects were excluded from this analysis due to the incorrect use of response buttons in the imagery task) (Figure 2). Pairwise comparisons showed that imagining a scene was neither statistically different in the congruent condition (mean ± SEM: 64.7% ± 3.2%) compared to the neutral condition (60.3% ± 4.8%; $t_{(12)} = 1.0$, $p = 0.34$) of experiment 2 nor statistically different in the identical condition (56.11% ± 3.7%) compared to the neutral condition (51.11% ± 4.6%; $t_{(14)} = 1.03$, $p = 0.32$) of experiment 3. However, imagining a scene was harder in the incongruent condition (80.6% ± 4.9%) versus the neutral condition (90.0% ± 3.2%; $t_{(14)} = -2.5$ [t, Student's t test], $p = 0.026$) of experiment 1 (Figure 2). No significant differences appeared in the ANOVA with the reaction times as dependent variable, nor did reaction times significantly differ between conditions of either experiment.

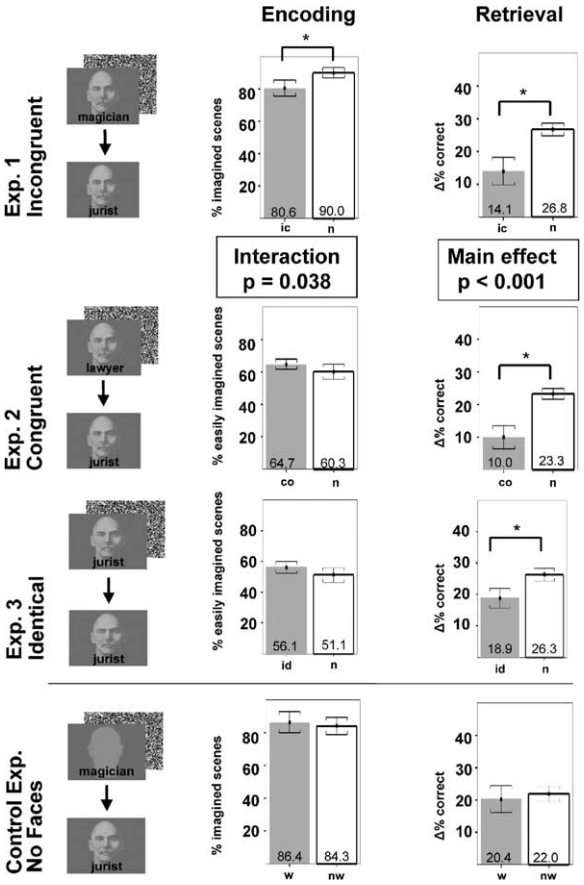

Figure 2. Behavioral Data

Behavioral performance data is given as the mean ± SEM for the explicit encoding tasks and for the cued recall of the explicitly learned professions. Encoding performance is indicated as the percentage of successfully imagined scenes (experiment 1 and behavioral control experiment) or as the percentage of scenes that could be imagined with ease (experiments 2 and 3). The retrieval performance is indicated as the percentage of correct professional categories above chance (50%) level. The icons to the left of the figure illustrate the implicit (with mask) and the subsequent explicit (without a mask) encoding during the experimental condition of each experiment. ic, incongruent condition; n, neutral condition; co, congruent condition; id, identical condition; w, a word (profession) had been subliminally presented along with a head contour; nw, a nonword had been subliminally presented along with a head contour.

Behavioral Control Experiment

There was no statistical difference in the "percentage of imagined scenes" between the experimental (86.4% ± 6.5%) and the neutral condition (84.3% ± 5.3%; $t_{(8)}$ = 0.62, p = 0.55; Figure 2), nor were there significant differences in the reaction times between conditions.

Retrieval

The performance measure was the percentage of correctly retrieved professional categories (academic or artist) minus 50% (50% = chance level).

Experiments 1, 2, and 3

An ANOVA with the factors Condition (experimental versus neutral condition) and Experiment (1, 2, or 3) and the dependent variable "percentage of correctly retrieved professional categories minus 50%" revealed a significant main effect ($F_{(1, 43)}$ = 30.19, p < 0.001) for Condition (Figure 2), but no significant interaction and no significant main effect for Experiment. Pairwise comparisons confirmed that retrieval performance was significantly reduced in the experimental condition versus the neutral condition of each fMRI experiment (M/SEM %; experiment 1: incongruent, 14.1/4.2; neutral, 26.8/1.9; $T_{(15)}$ = –3.12, p = 0.007; experiment 2: congruent, 10.0/3.5; neutral, 23.3/1.7; $T_{(14)}$ = –3.46, p = 0.004; experiment 3: identical, 18.9/3.2; neutral, 26.3/2.1; $T_{(14)}$ = –3.32, p = 0.005). No significant differences appeared in the ANOVA with the reaction times for correct answers as dependent variables, nor did the reaction times for correct answers differ significantly between conditions of either experiment.

Behavioral Control Experiment

There was no difference in the "percentage of correctly retrieved professional categories minus 50%" between the neutral (22.0% ± 2.4%) and the experimental conditions (20.4% ± 4.2%; $t_{(8)}$ = –0.26, p = 0.8; Figure 2). No significant differences appeared in the reaction times for correct answers between conditions.

Test of the Visual Presentation Threshold

Following the experiment, subjects underwent a structured interview about the visibility of the subliminal faces and words and a step-by-step debriefing while still situated in the dark MR scanner. None of the subjects reported awareness of the features of the subliminal stimuli or suspecting subliminal presentations during the visual detection task. We can therefore assume that the subliminal stimuli were presented below the threshold of subjective awareness (Cheesman and Merikle, 1984). To ascertain that stimuli were presented below the objective, and not only the subjective, awareness threshold (Cheesman and Merikle, 1984) of these subjects, they underwent a forced-choice visibility test at the end of the fMRI experiment. Forty-two of the 46 subjects who had participated in the three fMRI experiments performed this visibility test. Visibility data could not be collected in three subjects of experiment 1 and in one subject of experiment 2. The visibility test was carried out following rather than preceding the fMRI experiment in order to keep subjects unaware of subliminal presentations during the experiment and to test their visual discrimination accuracy at the point when they had gained the best visual expertise. Each subliminal stimulus was immediately followed by the forced-choice visibility test. This procedure is different from the fMRI experiment, in which four consecutive subliminal stimuli had been presented before their effect on explicit learning was measured. A potential conscious perception of a masked stimulus is likely captured by the trial-by-trial test procedure applied in the visibility test. If there were no measurable effects of conscious stimulus perception immediately following a masked trial, then it appears unlikely that such effects were present after a whole block of subliminal stimuli in the fMRI experiment. All psychophysical variables remained constant between the fMRI experiment and the visibility test.

An additional 30 face-profession pairs were pre-

sented subliminally to subjects. These were different from the pairs that had been presented to subjects during the experiment. The masked presentation of each face-profession pair was immediately followed by two forced-choice tasks. One forced choice was between the target and a distracter face and the other was between the two professional categories "academic" and "artist." In half of the trials, the face decision was presented first, counter-balanced across subjects. The order of the trials with the face decision first or the profession decision first was random. The percentage of correct answers of these 42 subjects was not significantly different from that of chance performance (= 50%) for both face decisions (49.32% ± 1.86%; $t_{(41)} = -0.366$, $p = 0.72$) and profession decisions (50.29% ± 1.11%; $t_{(41)} = 0.26$, $p = 0.8$), indicating that subjects were unable to discern visual features or derive word meanings. Because the subliminal stimuli of the behavioral control experiment had consisted of a head contour and a written profession (Figure 1A) in the experimental condition, we used another 30 head contour-profession pairs for this group's visibility test. Hence, their forced choices were only between the two professional categories "academic" and "artist." Subjects' percentages of correct answers indicated chance performance (53.5% ± 2.3%; $t_{(7)} = 1.548$, $p = 0.166$), suggesting that they were unable to grasp word meanings.

Because the subliminal effects between the experimental and neutral conditions of the fMRI experiments had originated in the processing of the subliminal words, it was the semantic test of the two forced-choice visibility tests which was the critical one. We therefore compared each subject's performance in the semantic (profession) forced-choice test to the one-tailed 5% cutoff (= 66.66% or 20/30 correct choices) of the chance distribution of correct choices. None of our subjects exceeded this cutoff.

To ensure that no stimulus or selection bias had contributed to the above results of the visibility test, we examined face and profession selections in 20 additional subjects, using the visibility test devoid of subliminal images. Instead, subliminal presentations consisted of a uniform gray screen. Subjects selected neither the target faces (51.75% ± 2.1%; $t_{(19)} = 0.84$, $p = 0.41$) nor the correct professional categories (51.65% ± 2.3%; $t_{(19)} = 0.73$, $p = 0.48$) with a better than chance (50%) accuracy. This suggests that there was no stimulus or response bias that might have masked a potential visibility effect in our experimental subjects. We therefore conclude that the masked stimuli were presented below the threshold of objective awareness in our experimental subjects (Cheesman and Merikle, 1984).

Neuroimaging Data

All data were thresholded at $p = 0.001$. We also included activity peaks with $p < 0.01$ if they were located in the region of interest, the medial temporal lobe, and we indicate this lower threshold where applicable.

Implicit Encoding Contrast

Brain activity underlying the implicit word processing and the implicit formation of semantic face-profession associations was revealed by comparing the fMRI signal associated with the masked presentations of face-profession pairs (incongruent, congruent, or identical condition) to the fMRI signal associated with the masked presentations of face-nonword pairs (neutral condition) for each experiment (Table 1).

Experiment 1: Incongruent

This comparison yielded significance in the activity data from the right anterior hippocampus/perirhinal cortex ($p < 0.01$; Figure 3), left inferior frontal gyrus, bilateral medial frontal gyri, left lingual/fusiform gyrus, left posterior fusiform gyrus, right lingual gyrus, bilateral cuneus, and the right caudate nucleus. The reversed comparison revealed an area of significant signal change in the left anterior hippocampus and, at the lower threshold ($p < 0.01$), also in the right hippocampus. Further activity changes were located in the left precentral gyrus and the right thalamus.

Experiment 2: Congruent

This comparison revealed activity peaks in the right (Figure 3) and left ($p < 0.01$) hippocampus, right temporal pole, right postcentral gyrus, and right fusiform gyrus. The reversed comparison showed activity peaks in the right perirhinal cortex ($p < 0.01$), right parahippocampal cortex ($p < 0.01$), and right superior temporal gyrus.

Experiment 3: Identical

This comparison yielded activity in the right and left (Figure 3) anterior hippocampus, right amygdala, bilateral superior temporal sulci and gyri, right middle temporal gyrus, left temporal insula, right middle and superior frontal gyri, bilateral precentral gyrus, bilateral cingulate gyrus, left inferior and left superior parietal lobule, right lingual gyrus, left cuneus, right globus pallidus, right thalamus, and left putamen. The reversed comparison revealed no significant activity.

Correlations between Implicit Encoding Contrast and Retrieval Impairment

For each experiment, we computed correlations between the individual implicit encoding contrasts (experimental versus neutral conditions) and the retrieval impairments expressed as the percentage of correct selections of profession in the neutral condition minus those in the experimental condition. The degree of the retrieval impairment is a strong measure of the impact that implicit memory had on explicit memory. This correlation reveals the key areas involved in the interaction between implicit and explicit memory (Table 2). Positive correlations imply that greater activity during implicit associative learning was related to greater explicit retrieval impairment.

Experiment 1: Incongruent

Peaks of significant positive correlations were located in the left (Figure 4) and right anterior hippocampus, left superior temporal gyrus, left inferior frontal gyrus, bilateral middle frontal gyri, and the left medial frontal gyrus. Significantly negative correlations were found in the left uncus, right insular cortex, and right caudate nucleus.

Experiment 2: Congruent

Peaks of significant positive correlations were situated in the left anterior hippocampus (Figure 4), left amygdala, and left inferior frontal gyrus.

Significantly negative correlations were located in the

Table 1. Implicit Encoding Contrast

Brain Region	Left/Right	BA[a]	MNI Coordinates (mm) x	y	z	T[b]
One-Sample t Tests						
Experiment 1: Incongruent						
Incongruent > Neutral						
Hippocampus/perirhinal cortex	R		34	−10	−28	4.0*
Inferior frontal gyrus	L	45	−34	32	6	5.34
Medial frontal gyrus	R	9	8	58	18	4.03
Medial frontal gyrus	L	10	−4	54	6	3.99
Lingual/fusiform gyrus	L	37	−18	−52	−14	5.88
Lingual gyrus	R	18/19	6	−66	4	4.71
Fusiform gyrus	L	19	−22	−90	−4	5.07
Cuneus	L	18	−16	−86	22	4.14
Cuneus	R	18	8	−86	26	4.40
Caudate nucleus	R		18	6	16	4.79
Incongruent < Neutral						
Hippocampus	L		−28	−18	−12	5.08
Hippocampus	R		34	−26	−14	3.1*
Precentral gyrus	L	6	−34	4	36	4.27
Thalamus	R		14	−16	14	4.17
Experiment 2: Congruent						
Congruent > Neutral						
Hippocampus	R		30	−22	−12	4.82
Hippocampus	R		36	−32	−12	3.4*
Hippocampus	L		−20	−12	−14	3.7*
Hippocampus	L		−30	−26	−14	2.7*
Temporal pole	R	38	46	12	−30	4.07
Postcentral gyrus	R	1	60	−14	12	4.19
Fusiform gyrus	R	37	38	−54	−26	4.56
Congruent < Neutral						
Perirhinal cortex	R		28	−4	−34	3.4*
Parahippocampal cortex	R	35	24	−42	−2	3.0*
Superior temporal gyrus	R	22	46	−44	16	4.44
Experiment 3: Identical						
Identical > Neutral						
Hippocampus	L		−30	−14	−18	6.15
Hippocampus	R		30	−8	−18	4.73
Amygdala	R		20	−2	−16	5.22
Superior temporal sulcus	R		62	−44	10	5.68
Superior temporal sulcus	R		48	−30	−4	4.98
Superior temporal sulcus	L		−48	−30	−4	3.97
Superior temporal sulcus	L		−64	−48	6	4.50
Superior temporal gyrus	L	22	−62	0	0	4.22
Superior temporal gyrus	R	22	56	−48	20	4.05
Middle temporal gyrus	R	21	40	−68	18	4.45
Temporal insula	L		−34	−20	0	5.46
Middle frontal gyrus	R	6	36	10	44	5.03
Superior frontal gyrus	R	6	12	−6	66	5.22
Superior frontal gyrus	R	8	16	44	42	5.00
Precentral gyrus	L	4	−40	−20	34	4.72
Precentral gyrus	R	4	54	−10	16	4.66
Cingulate gyrus/paracentral lobule	L	31/5	−16	−26	46	6.44
Cingulate gyrus	R	24	6	−8	38	5.14
Inferior parietal lobule	L	40	−48	−28	22	4.24
Superior parietal lobule	L	7	−30	−44	50	4.27
Lingual gyrus	R	18	14	−76	−10	4.84
Cuneus	L	18	−8	−94	24	4.38
Globus pallidus	R		14	−28	12	4.96
Thalamus	R		24	−20	8	6.73
Putamen	L		−26	−24	2	4.13
Identical < Neutral						
No significant difference						

*$p < 0.01$.

[a] BA, Brodmann Area.

[b] Student's t test, values of peaks within significantly activated clusters of voxels ($p < 0.001$).

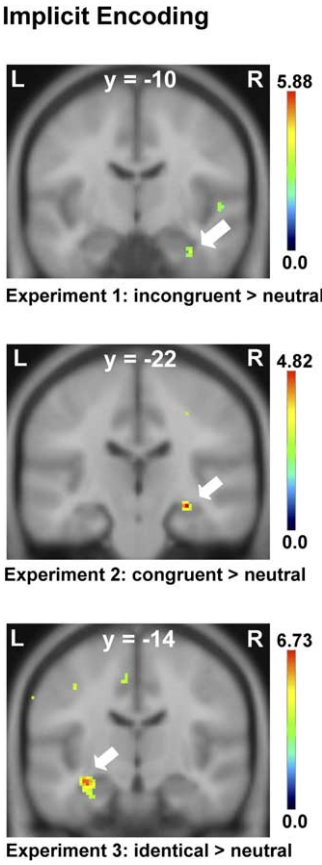

Figure 3. Implicit Encoding Contrasts

Hippocampal effects (arrows) resulting from the comparison of the fMRI data in the experimental versus the neutral implicit encoding condition are shown for each fMRI experiment. MR signal differences are displayed in color-coded t-values (see bar) and presented on coronal sections of the T1-weighted MNI-template of SPM. The anterior-posterior location of each section is indicated by the y MNI coordinate. L/R, left/right side of brain.

right and left ($p < 0.01$) anterior hippocampus, bilateral superior temporal sulci, left inferior temporal gyrus, and right superior frontal gyrus.

Experiment 3: Identical

Peaks of significant positive correlations were situated in the left superior temporal sulcus, right middle frontal gyrus, right inferior parietal lobule, bilateral precuneus, and left cingulate gyrus. Significantly negative correlations were found in the right anterior subiculum/hippocampus (Figure 4), left inferior temporal sulcus, and left middle frontal gyrus.

Correlations between Implicit Encoding Contrast and Explicit Encoding Facilitation

We computed correlations for each experiment between the individual implicit encoding contrasts (experimental versus neutral conditions) and the explicit encoding facilitation expressed as the difference in the percentage of (easily) imagined scenes between the experimental and the neutral condition. This correlation shows the extent to which implicit encoding activity relates to the subject's ability to imagine the same person (as subliminally presented) acting in a scene typical of the same (experiment 3), a congruent (experiment 2), or an incongruent (experiment 1) profession (Table 3). Positive correlations imply that greater activity during implicit associative learning was related to a greater ease with imagery.

Experiment 1: Incongruent

Peaks of significant positive correlations were found in the left parahippocampal cortex, left inferior temporal gyrus, left inferior frontal gyrus, left superior parietal lobule, and left postcentral gyrus. Significantly negative correlations were situated in the right temporal insula, right inferior temporal gyrus, left superior temporal sulcus, right superior temporal gyrus, left superior frontal gyrus, right superior parietal lobule, left intraparietal sulcus, bilateral postcentral gyrus, and right precentral gyrus.

Experiment 2: Congruent

Peaks of significant positive correlations were located in the right superior parietal lobule, right retrosplenial cortex, and right brain stem. There were no significant negative correlations.

Experiment 3: Identical

Peaks of significant positive correlations were found in the left and right hippocampus, right entorhinal cortex, left parahippocampal cortex, right middle frontal gyrus, left superior parietal lobule, right fusiform gyrus, and left inferior occipital gyrus. Significantly negative correlations were located in the left superior temporal sulcus, right superior temporal gyrus, and right anterior cingulate gyrus.

Explicit Encoding Contrast

The influence that implicit associative learning had on explicit associative learning can also be captured in the explicit encoding contrast (experimental condition versus neutral condition) (Table 4).

Experiment 1: Incongruent

The explicit encoding contrast yielded significance in the right anterior hippocampus, right parahippocampal cortex, right superior frontal gyrus, and left fusiform gyrus. The reversed comparison revealed significance in the right inferior temporal gyrus and the left precentral gyrus.

Experiment 2: Congruent

This comparison revealed significant activity in the right middle temporal gyrus, left temporal insula, right superior frontal gyrus, right postcentral gyrus, right retrosplenial cortex, right caudate nucleus, and right precuneus. The reversed comparison yielded significance in the right anterior hippocampus ($p < 0.01$), right perirhinal cortex ($p < 0.01$), and right inferior parietal lobule.

Experiment 3: Identical

The explicit encoding contrast yielded activity peaks in the right and left ($p < 0.01$) perirhinal cortex/hippocampus, right superior temporal gyrus, left middle temporal gyrus, bilateral inferior frontal gyri, right superior frontal gyrus, right precentral gyrus, left middle and medial frontal gyri, left postcentral gyrus, bilateral superior and inferior parietal lobules, left globus pallidus, and right putamen. The reversed comparison revealed no significance.

Table 2. Correlations between Implicit Encoding Contrast (Experimental minus Neutral Condition) and Retrieval Impairment (Recall Neutral minus Experimental Condition)

Brain Region	Left/Right	BA[a]	MNI Coordinates (mm) x	y	z	T[b]
Correlation Analysis						
Experiment 1: Incongruent						
Positive Correlations						
Hippocampus	L		–16	–10	–24	5.57
Hippocampus/amygdala	R		12	–8	–18	4.21
Hippocampus	R		30	–22	–12	4.12
Superior temporal gyrus	L	22	–48	–50	26	4.10
Inferior frontal gyrus	L	45	–44	30	8	3.80
Middle frontal gyrus	R	46	40	48	18	4.13
Middle frontal gyrus	R	6	24	0	48	4.13
Middle frontal gyrus	L	10	–40	46	–6	3.98
Medial frontal gyrus	L	8	–8	36	34	4.36
Negative Correlations						
Uncus	L	34	–22	6	–28	3.90
Temporal insula	R		38	–16	14	3.80
Caudate Nucleus	R		12	4	14	3.80
Experiment 2: Congruent						
Positive Correlations						
Hippocampus	L		–18	–10	–16	3.87
Amygdala	L		–14	–8	–20	3.99
Inferior frontal gyrus	L	47	–26	20	–10	4.12
Negative Correlations						
Hippocampus	R		34	–18	–18	4.33
Hippocampus	L		–30	–22	–14	3.2*
Superior temporal sulcus	L		–58	0	–10	3.87
Superior temporal sulcus	L		–60	–10	–12	4.35
Superior temporal sulcus	R		66	–14	–8	4.42
Inferior temporal gyrus	L	20	–48	–30	–18	4.54
Superior frontal gyrus	R	6	20	–10	64	4.10
Experiment 3: Identical						
Positive Correlations						
Superior temporal sulcus	L		–54	–42	8	6.32
Middle frontal gyrus	R	46	34	42	20	4.84
Inferior parietal lobule	R	40	54	–46	36	5.17
Precuneus	L	7	–12	–58	52	5.02
Precuneus	L	7	–8	–44	50	4.69
Precuneus	L	7	–14	–68	36	4.03
Precuneus	R	7	12	–74	48	4.26
Cingulate gyrus	L	23	–6	–16	30	9.71
Negative Correlations						
Subiculum/hippocampus	R		22	–12	–28	3.02*
Inferior temporal sulcus	L		–52	–12	–28	4.24
Middle frontal gyrus	L	6	–30	18	62	5.01

*$p < 0.01$.
[a] BA, Brodmann Area.
[b] Student's t test, values of peaks within significantly activated clusters of voxels ($p < 0.001$).

Discussion

The postexperimental interviews and the forced-choice visibility tests confirmed that subjects had no awareness of the subliminal faces and words suggesting that the subliminal information was presented below the threshold of objective awareness (Cheesman and Merikle, 1984). During subliminal presentations, subjects engaged in a visual detection task that directed their gaze to a spot between the eyes of the face stimuli. Detection accuracies indicated that subjects had fixated their gaze and maintained a constantly high level of visual attention throughout the experiments, which may have facilitated the processing of the subliminal information.

Our behavioral and imaging findings suggest that the subliminal face-profession pairs were processed via the hippocampus and that this implicit processing interacted with the subsequent explicit processing. We suggest that the critical implicit process was the implicit formation of semantic face-word associations for the following reasons. Our implicit experimental conditions allowed for implicit face perception, implicit word processing, and the implicit formation of semantic, phonological, and visual associations between words and faces. Implicit face perception and the implicit formation of visual and phonological associations between words and faces are unlikely sources of the implicit-explicit interactions because these processes were possible in both the experimental and neutral con-

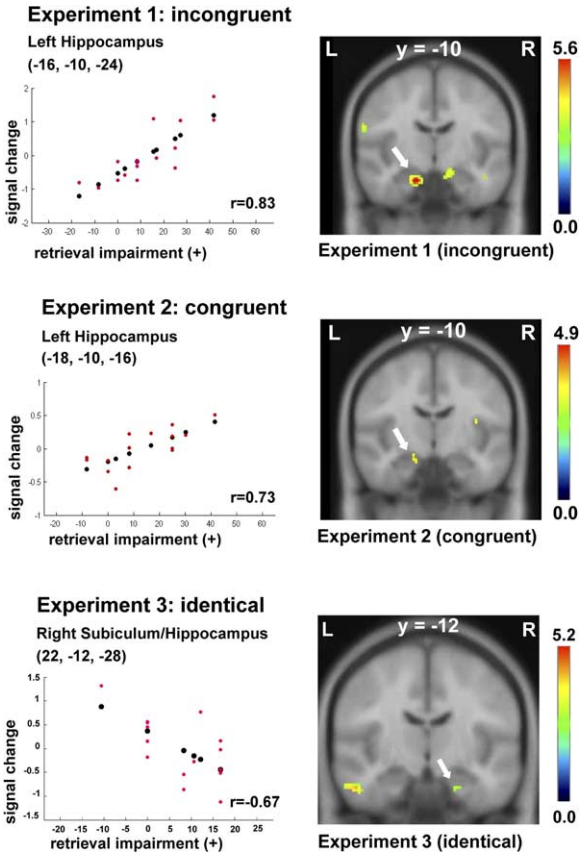

Figure 4. Correlations between the Implicit Encoding Contrasts and Retrieval Impairment

Correlations were computed between the individual implicit encoding contrasts (experimental versus neutral condition) and the later retrieval impairment expressed as % correctly retrieved professional categories in the neutral condition minus the experimental condition (positive values stand for retrieval impairment in the experimental condition). The correlation results in the hippocampus (arrows) are shown for each fMRI experiment in scatter plots and as color-coded t-values (see bar) superimposed on coronal sections of the T1-weighted MNI-template of SPM. The anterior-posterior location of each correlation peak is indicated by the y MNI coordinate. L/R, left/right side of brain.

ditions of the experiments. Neither can implicit word processing account for the implicit-explicit interactions because the subliminal words alone had no effect on explicit learning in the behavioral control experiment. We therefore conclude that the implicit-explicit interactions must have originated in the implicit formation of semantic face-word associations. These could only be formed in the experimental conditions. This interpretation is underscored by the behavioral and fMRI data. Subjects experienced significant difficulties in imagining individuals in occupations that were incongruous to the previously presented subliminal occupations. When, however, the supraliminal and subliminal professions were semantically congruous or identical, there were no such difficulties. If anything, imagining scenes was facilitated, but this effect did not reach statistical significance. Nevertheless, an inhibitory/facilitative effect of incongruous/congruous subliminal face-word pairs on explicit learning also became apparent in the direction of the correlations between implicit encoding contrasts and the imagination data. Correlations were primarily negative in the incongruous condition (the more implicit encoding activity, the worse the imagination performance) but positive in the congruous and the identical conditions. Thus, depending on the semantic congruency of words, there were opposite effects of implicit learning on explicit learning. These findings indicate that the implicit-explicit interactions had originated in the implicit formation of individual semantic face-profession associations. This finding is important because earlier findings had cast doubts on the feasibility of implicitly forming associations within just one trial (Bowers and Schacter, 1990; McKone and Slee, 1997; Musen and Squire, 1993; Squire, 1992a). On the other hand, the current results are consistent with our previous findings that are suggestive of one-trial implicit, semantic, paired-associate learning (Henke et al., 2003a, Henke et al., 2003b).

While implicit encoding interacted differentially with explicit encoding depending on the semantic congruency of words, explicit retrieval was significantly impaired in the experimental versus the neutral conditions of all experiments. Classic repetition priming from subliminal to supraliminal stimuli is not a likely reason for this impairment, because explicit encoding in the experimental condition was not associated with a significant repetition suppression of the BOLD signal, as would be expected during the processing of a primed stimulus (Henson, 2003; Schacter and Buckner, 1998a, Schacter and Buckner, 1998b). On the contrary, BOLD signals were enhanced rather than decreased in the experimental versus the neutral explicit encoding conditions. This may reflect at least two things: the encoding of a greater number of stimulus aspects, yielding a better retrieval performance, which was not the case, or increased computational demands at explicit encoding due to competing implicit and explicit processes. The latter interpretation is supported by the significant correlations ($p < 0.001$) which were all positive, and never negative, in each experiment between the explicit encoding contrasts (experimental versus neutral condition) and the retrieval impairment in the experimental condition (data not shown). These positive correlations were situated mainly in the frontal and temporal lobes. The larger the signal enhancement was during explicit encoding, the greater was the explicit retrieval impairment. The assumed implicit-explicit competition may have been emanating from the recovery of implicit memory traces when subjects confronted again with the same faces during the imagery task started to compare the face-associated implicit learning with the currently available explicit information. Although a word presented with the supraliminal face may be congruous or even identical with the previously associated subliminal word, the word's different representational status—conscious versus nonconscious—may suffice to create interference. We assume that this general implicit-explicit interference effect occurred simultaneously with the specific semantic relatedness effect (discussed above) at the time of explicit learning. The resultant effects on performance in the imagery task were thus double negative (–, –) in the incongruous condition,

Table 3. Correlations between Implicit Encoding Contrast (Experimental versus Neutral Condition) and Explicit Encoding Facilitation (% [easily] Imagined Scenes Experimental minus Neutral Condition)

Brain Region	Left/Right	BA[a]	MNI Coordinates (mm) x	y	z	T[b]
Correlation Analysis						
Experiment 1: Incongruent						
Positive Correlations						
Parahippocampal cortex	L	35	−24	−54	−6	5.59
Inferior temporal gyrus	L	37	−48	−66	−2	5.70
Inferior frontal gyrus	L	9	−38	18	34	4.42
Superior parietal lobule	L	7	−10	−54	64	5.21
Postcentral gyrus	L	7	−10	−46	66	4.54
Negative Correlations						
Temporal insula	R		38	−16	10	5.37
Inferior temporal gyrus	R	20	50	−30	−22	5.43
Superior temporal sulcus	L		−62	−24	−4	4.68
Superior temporal sulcus	L		−56	−40	8	4.68
Superior temporal gyrus	R	22	66	−18	10	4.86
Superior frontal gyrus	L	6	−4	−18	50	4.73
Superior parietal lobule	R	7	22	−58	70	4.33
Intraparietal sulcus	L	7	−34	−42	50	4.24
Postcentral gyrus	R	2	48	−20	20	6.12
Postcentral gyrus	L	2	−46	−28	58	5.86
Precentral gyrus	R	4	52	−6	10	4.83
Experiment 2: Congruent						
Positive Correlations						
Superior parietal lobule	R	7	26	−68	58	5.24
Retrosplenial cortex	R	30	14	−54	16	4.61
Brain stem	R		4	−28	−30	5.14
Negative Correlations						
No significance						
Experiment 3: Identical						
Positive Correlations						
Entorhinal cortex	R		22	−26	−22	6.57
Parahippocampal cortex	L	35	−28	−44	−6	6.40
Hippocampus	L		−18	−36	2	4.36
Hippocampus	L		−24	−26	−14	4.34
Hippocampus	R		36	−30	−6	3.7*
Middle frontal gyrus	R	6	38	12	54	4.87
Superior parietal lobule	L	7	−36	−52	50	4.46
Fusiform gyrus	R	36	26	−36	−30	5.84
Fusiform gyrus	R	19	36	−74	−24	4.23
Inferior occipital gyrus	L	19	−42	−90	2	4.84
Negative Correlations						
Superior temporal sulcus	L		−52	−6	−10	5.00
Superior temporal gyrus	R	22	66	−34	10	4.58
Anterior cingulate	R	32	14	44	4	4.89

*$p < 0.01$.
[a] BA, Brodmann Area.
[b] Student's t test, values of peaks within significantly activated clusters of voxels ($p < 0.001$).

which might explain the significant difficulty with the imagery task. In the congruous and identical conditions, however, the resultant effects were both negative and positive (–, +), which might explain the nonsignificant effects on performance of the imagery task in these experiments. Following explicit encoding, the formed implicit and explicit memory traces for a given face were probably undergoing consolidation during the 5–15 min interval between encoding and retrieval portions of the study. The consolidation process may have amplified any competition between implicit and explicit memory traces, while the initial semantic relatedness effect may have worn off. This may have resulted in the clear impairment of explicit retrieval, irrespective of the semantic relatedness of the subliminal and supraliminal words. It should be noted that our subjects were screened for good performance on retrieval of explicit memory (see Experimental Procedures). It is conceivable that a good associative learning system is well capable of forming associations even implicitly and therefore suffers from greater interference by implicit associations than a less capable associative learning system would. The physiological mechanisms involved in this implicit-explicit interaction are unknown. In fact, these are the first imaging experiments addressing interactions between implicit and explicit memory processes involving the medial temporal lobe, to our knowledge. For explicit memory, however, it is well established that repeated versus one-time processing of congruous or identical information leads to

Table 4. Explicit Encoding Contrast

Brain Region	Left/Right	BA[a]	MNI Coordinates (mm) x	y	z	T[b]
One-Sample t Tests						
Experiment 1: Incongruent						
Incongruent > Neutral						
Hippocampus	R		32	−12	−22	3.92
Parahippocampal cortex	R		20	−56	0	3.90
Superior frontal gyrus	R	9	24	58	34	4.00
Fusiform gyrus	L	19	−22	−76	−18	4.08
Incongruent < Neutral						
Inferior temporal gyrus	R	20	54	−38	−20	5.72
Inferior temporal gyrus	R	37	62	−56	−18	4.48
Precentral gyrus	L	6	−34	4	30	4.39
Experiment 2: Congruent						
Congruent > Neutral						
Middle temporal gyrus	R	39	44	−66	16	4.55
Temporal insula	L		−30	−22	12	4.06
Superior frontal gyrus	R	6	14	−2	64	3.99
Postcentral gyrus	R	1	44	−20	34	4.82
Retrosplenial cortex	R	30	20	−52	12	5.05
Caudate nucleus	R		22	22	0	4.83
Precuneus	R	31	24	−64	22	4.23
Congruent < Neutral						
Hippocampus	R		38	−14	−22	3.0*
Perirhinal cortex	R		26	−2	−34	2.9*
Inferior parietal lobule	R	40	68	−42	30	4.30
Experiment 3: Identical						
Identical > Neutral						
Perirhinal cortex/hippocampus	R		42	−6	−30	5.39
Perirhinal cortex/hippocampus	L		−28	−8	−30	3.3*
Superior temporal gyrus	R	38	62	12	−2	4.23
Middle temporal gyrus	L	21	−68	−36	0	5.20
Inferior frontal gyrus	R	44	58	10	8	5.22
Inferior frontal gyrus	R	47	42	22	−12	4.54
Inferior frontal gyrus	L	47	−30	18	−10	4.12
Superior frontal gyrus	R	6	12	22	58	4.80
Middle frontal gyrus	L	6	−30	−6	46	4.73
Medial frontal gyrus	L	6	−4	−6	56	4.63
Precentral gyrus	R	6	52	2	38	4.83
Postcentral gyrus	L	1	−66	−12	26	4.43
Superior parietal lobule	R	7	46	−40	64	4.81
Superior parietal lobule	L	7	−38	−54	64	4.76
Inferior parietal lobule	R	40	62	−34	48	4.36
Inferior parietal lobule	L	40	−56	−28	38	4.17
Globus pallidus	L		−16	−26	0	6.14
Putamen	R		24	8	10	5.17
Identical < Neutral						
No significant difference						

*$p < 0.01$.
[a] BA, Brodmann Area.
[b] Student's t test, values of peaks within significantly activated clusters of voxels ($p < 0.001$).

improvement, and not impairment, of retrieval performance (Ebbinghaus, 1992).

The fMRI signal recorded during implicit face-profession learning versus implicit face-nonword learning was enhanced within the anterior hippocampus in each experiment (Figure 3). Explicit face-profession learning also yielded robust signal increases in the bilateral anterior hippocampus in all experiments (data not shown). These results along with previous findings (Chun and Phelps, 1999; Curran, 1997; Henke et al., 2003a, Henke et al., 2003b; McIntosh et al., 2003; Rajaram and Coslett, 2000a, Rajaram and Coslett, 2000b; Rose et al., 2002; Savage et al., 2002; Schendan et al., 2003; Yang et al., 2003) suggest a role for the hippocampus not only in explicit but also implicit relational learning. Notably, the notion of the hippocampus as a relational processor came primarily from animal experiments (Cohen and Eichenbaum, 1993; Bunsey and Eichenbaum, 1996; Dusek and Eichenbaum, 1997; Rolls and Treves, 1998) in which conscious awareness of learning and retrieval is not as much a topic as it is in the human literature. The animal and human data together may extend the classic views of memory systems that do not posit a role for the hippocampus in implicit memory (Graf and Schacter, 1985; Squire, 1992a, Squire, 1992b; Squire and Zola-Morgan, 1991). The contrasts of im-

plicit face-profession learning versus implicit face-nonword learning also yielded enhanced activity in several neocortical areas including the temporal and prefrontal cortices known to mediate lexical-semantic analyses necessary for word comprehension. These results varied between the three fMRI experiments, even though the contrasts should isolate equal implicit processes. The likely reason for this variability is the different imaging protocols used in the three fMRI experiments. Our 3T Philips Intera whole-body system and the imaging protocols were improved during the course of the study. We started out with conventional echo-planar imaging in experiment 1 (incongruent), in which no differences in lateral temporal activity were apparent, and went on to parallel imaging with SENSE in experiments 2 (congruent) and 3 (identical), in which differences in lateral temporal activity became apparent. SENSE reduces image distortions and susceptibility artifacts in the temporal lobes, saving signal that can be compared across conditions (Preibisch et al., 2003; Schmidt et al., 2005). Furthermore, experiments 1 and 2 were performed with the "Master" gradient system, whereas experiment 3 was performed with the "Triade" gradient system. The latter allows for faster data acquisition and therefore enhanced gradient-echo EPI quality.

We correlated the individual implicit encoding contrasts (face-profession learning versus face-nonword learning) with the degree of the explicit retrieval impairment for each experiment to reveal the brain areas associated with the interaction between implicit and explicit memory. These correlations yielded significance in the anterior hippocampus in all three experiments (Figure 4). Thus, the degree of the hippocampal engagement in the implicit encoding of face-profession pairs versus face-nonword pairs related to the degree of the explicit retrieval deficit. This result is important because it suggests that the hippocampus was not merely coactivated during masked presentations, but changed its engagement relative to the negative effects that implicit memory had on explicit memory. The anterior location of the correlation and subtraction results within the hippocampus corresponds to previous evidence of an anterior hippocampal engagement in explicit semantic associative learning (Henke et al., 1997, Henke et al., 1999, Henke et al., 2003a; Schacter and Wagner, 1999; Sperling et al., 2001, Sperling et al., 2003). We therefore assume that the anterior part of the hippocampus participates in both the explicit and implicit formation of new semantic associations. Further, correlation sites in the three experiments were situated in the left lateral temporal cortex, left inferior frontal gyrus (Brodmann Areas [BAs] 45 and 47), middle frontal gyrus (BAs 46 and 10), medial frontal gyrus (BA 8), and superior frontal gyrus (BA 6). These temporal-frontal regions have been implicated in the *semantic* processing of verbal and pictorial supraliminal stimuli in previous neuroimaging studies (e.g., Devlin et al., 2002; Grabowski et al., 2001; Martin and Chao, 2001; Perani et al., 1999; Pilgrim et al., 2002; Vandenberghe et al., 1996; Wagner et al., 2001). Therefore, these correlation results might suggest that the better the masked words were understood and semantically related to faces, the more detrimental was their effect on explicit retrieval. This finding underscores our earlier conclusion that the effect of implicit memory on explicit memory originated in the implicit formation of semantic rather than visual or phonological associations between words and faces.

Remarkably, medial temporal activity changes during the masked experimental versus the neutral conditions were bidirectional (Table 1). We have previously observed bidirectional hippocampal signal changes during the masked presentation of face-profession pairs versus masked presentation of single items (Henke et al., 2003b) and propose the following reason for this phenomenon. During masked presentations, hippocampal neurons engage not only in the encoding of the masked stimuli but also in the spontaneous encoding of the omnipresent conscious thoughts (Stark and Squire, 2001). If hippocampal neurons additional to those engaged in the encoding of conscious thoughts turn to encode the masked stimulus pairs as soon as the experimental condition begins, then activity in the experimental condition rises over the activity in the neutral condition. If, however, those neurons that are engaged in the encoding of conscious thoughts happen to be neurons specialized in the encoding of face-profession pairs, then at least a subgroup of these neurons will stop encoding conscious thoughts and switch over to encoding masked face-profession pairs when the experimental condition begins. This switch will effectively decrease activity in that area during the experimental versus the neutral condition because the neural responses evoked by masked stimuli are interrupted by the masks (Kovacs et al., 1995; Rolls and Tovee, 1994), which likely decreases the BOLD signal. We assume that the balance of implicit and explicit encoding activity in the hippocampus depends on the type of masked stimuli (pairs versus single items) and the type of simultaneous conscious mental activity. Although our subjects engaged in a visual detection task during masked conditions, they were still free to have their own thoughts.

These and previous findings of implicit relational learning may modify the view that conscious awareness is necessary for snapshot associative learning (Bowers and Schacter, 1990; McKone and Slee, 1997; Musen and Squire, 1993; Squire, 1992a). The implicit semantic associations of the present experiments were formed "on the fly," within just one trial. Rapid associative learning has been considered characteristic of hippocampal learning, as opposed to neocortical learning, which is viewed as incremental and slow (Norman and O'Reilly, 2003; O'Reilly and Rudy, 2000; Rolls and Treves, 1998). We assume that rapid semantic associative learning invariably engages the hippocampus, mainly in its anterior aspect, independently of stimulus awareness. The current and earlier results (Greene et al., 2001; Willingham, 1997) may also extend the prevailing view that implicitly formed associations consist of rigid, fused, or noncompositional representations, whereas explicitly formed associations are flexible and compositional and allow for generalization (e.g., Cohen and Eichenbaum, 1993; Dienes and Berry, 1997; Squire, 1992a; but see Cohen et al., 1999). Flexibility and compositionality have been considered key features of hippocampal processing (Cohen and Eichenbaum, 1993; Eichenbaum et al., 1996). For the present argument, it should be kept in mind that the trials in our experiments

consisted of blocks of four subliminal face-profession pairs, immediately followed by blocks of the four corresponding supraliminal counterparts that were presented in the same order. This design requires that each subliminal face be linked to its profession in a *compositional* way to make possible the interference that we observed in the incongruent condition: at the time of explicit learning, a face A must be retrieved as an individual component in order to be identified as the common piece of information present in the implicit A – B and the explicit A – C stimulus pair. In addition, the implicit association A – B must be reactivated and compared in terms of semantic congruency to the supraliminal item pair A – C in order to produce a semantic interference with explicit encoding, as observed in experiment 1.

These results have implications for theories of memory systems. The division between hippocampus-dependent and -independent memories along the dimension of awareness (implicit versus explicit) had been motivated by the initial findings of preserved implicit memory skills—other than rapid semantic associative learning—in hippocampal amnesic patients (Corkin, 1968; Cohen and Squire, 1980; Milner et al., 1968; Warrington and Weiskrantz, 1968). Yet, it may be that the computational characteristics of the hippocampus, and not the level of conscious awareness, determine whether the hippocampus is or is not involved in a memory task.

Experimental Procedures

Subjects

Fifty-five students, all males with normal eyesight, participated in the four experiments. They did not report past or current psychiatric or neurological problems or use of drugs or medication and demonstrated good retrieval performance in the neutral conditions of the experiments used in this study. We adopted a retrieval criterion of at least 66.66% correct (50% = chance)—which corresponds to 8 of 12 correctly retrieved associations—in the neutral condition, because a poorer retrieval performance would not permit measurement of a potential impairment effect of the subliminal stimuli on explicit learning/retrieval in the experimental condition. Of these 55 subjects, 16 participated in experiment 1 (all right-handed; mean age ± SD: 24 ± 2.4 years; range, 21–29 years), 15 in experiment 2 (all right-handed; 24.4 ± 2.55 years; range, 21–29 years), 15 in experiment 3 (all right-handed; 24.1 ± 2.4 years; range, 20–29 years) and 9 in the behavioral control experiment (6 right-handed, 1 left-handed, 2 ambidexters; 25 ± 2.1 years; range, 23–29 years). Written informed consent was obtained prior to all experiments. Yet, subjects were only informed after the experiments that stimuli had been briefly flashed between masks. The study was approved by the Ethics Committee of the Kanton of Zurich.

Procedure

Experiments 1–3 consisted of two fMRI time series with blocked trials, one time series for encoding and one for retrieval, separated by a 5 min interval (Figure 1). The same procedure was applied to the behavioral control experiment, which was also conducted in the MR scanner but no MR data were collected. Following interviews and paper work, the subjects in all four experiments were situated in the completely darkened MR scanner to allow their eyes to adapt to the dark. Then they practiced the experimental tasks, performed those tasks, went through the postexperimental debriefing, and finally took the forced-choice tests to evaluate the presentation threshold used. In both the encoding and the retrieval parts of all experiments, twelve stimuli were presented per condition, divided into three blocks of four trials. Each trial lasted 6 s: unmasked stimuli were presented during the entire 6 s time window, while masked stimuli were presented 12 times for 17 ms between masks and fixation slides within the 6 s time window. The order of trials per condition and the order of conditions per time series were varied between subjects to avoid systematic order effects. However, each block of four explicit learning trials was always immediately preceded by the block containing the corresponding implicit learning trials. The four stimuli of an implicit learning block were presented in the same order as the corresponding four stimuli presented in the following explicit learning block to ensure a constant delay of 18 s between each subliminal stimulus and its supraliminal counterpart. Stimulus sets used for learning and retrieval were rotated over conditions to distribute stimulus-generated effects.

Tasks

Implicit Learning

The sequences with masked presentations were introduced to subjects as a visual detection task. This was in fact the task that engaged subjects while they viewed the subliminal presentations. Between the presentations of subliminal stimuli and masks, a fixation slide was presented at 1 s intervals. This black fixation slide contained either a central white cross or, in one-sixth of the presentations, a central white horizontal or vertical bar. The central location corresponded to the midpoint between the eyes of the subliminal faces. The task that engaged the subjects' conscious attention was to detect and indicate by button press the occurrence of a horizontal or vertical bar. Blocks of masked presentations were announced by a 2 s presentation of the letter "d" for "detection task."

Explicit Learning

In order to achieve a comparable encoding quality and quantity among subjects, they were instructed in the encoding strategy in all experiments. It required subjects to imagine each person presented acting in a scene of the indicated profession. This imagery task automatically induces a semantic processing of faces and words and a semantic face-word binding. In experiment 1 and the behavioral control experiment, subjects indicated by button press whether they could or could not imagine a scene as instructed. Because this instruction yielded approximately 90% affirmative answers in these initially performed experiments, we changed this instruction for the subsequently performed experiments 2 and 3 to achieve a more even response distribution, which leaves room for a potential increase in the number of positive responses. Instructions for experiments 2 and 3 required subjects to indicate by button press whether they found it easy or hard to imagine a presented person in a scene of the indicated profession. Blocks of explicit learning were announced by a 2 s presentation of the letter "i" for "imagery task".

In the explicit baseline condition of all experiments, head contours were presented with the instruction to indicate by button press whether the area of the left or the right ear was larger. These task blocks were announced by a 2 s presentation of the letter "e" for "ear task."

Explicit Retrieval

The faces that had been learned explicitly during the experimental and neutral encoding conditions were presented again during the experimental and neutral retrieval conditions, respectively. Faces acted as cues for the explicit recall of the associated professions. Subjects indicated the superordinate professional category—academic or artist—by button press. The baseline condition consisted of the ear task (see above).

Stimuli and Masking Paradigm

Stimuli were adopted from Henke et al. (2003b) and consisted of 48 black and white full frontal portraits of unknown bald individuals with neutral facial expressions (Kayser, 1985). Stimuli were digitized and degraded in contrast for the subliminal presentations; the same low-contrast images were also used for the supraliminal presentations (Figure 1). Ten academic and ten artistic professions were assigned to faces in a way that the appearance of individuals was not indicative of their professions (Figure 1A). The 48 face-profession pairs were divided into four sets of 12 stimuli for use in

the explicit encoding conditions. For implicit encoding, three variants of each set were created. For the incongruous implicit condition of experiment 1, faces were combined with a profession of the opposite professional category (e.g., explicit: singer [artist]; implicit: physician [academic]). For the congruent implicit condition of experiment 2, faces were combined with semantically close professions from either the same semantic level (e.g., engineer-architect, pianist-organist) or from the subordinate level (e.g., physician-surgeon, singer-soprano). For the implicit neutral conditions, faces were combined with nonwords (e.g., bdfper), which had numbers of letters comparable to those in the words for the written professions. Although they were pronounceable, they did not sound like German words. For the explicit baseline task, head contours (Figure 1) were created such that the area of either the right or the left ear was larger. In the implicit baseline task, one of these head contours was repeatedly presented. This same head contour was combined with written professions and nonwords for the implicit conditions of the behavioral control experiment.

The masks consisted of 40 black and white visual noise images from Henke et al. (2003b). The three fixation slides used for the visual detection task contained a black background with either a white cross or a white horizontal or vertical bar. We used the masking technique of Henke et al. (2003b), in which a stimulus (S) was presented 12 times within 6 s for 17 ms. Visual noise masks (M) were presented for 183 ms and the fixation cross or the vertical/horizontal bar (F), for 233 ms. The stimulation sequence for one trial (6 s) was F - M - S - M - M - S - M - F - M - S - M - M - S - M - F - M - S - M - M - S - M - F - M - S - M - M - S - M - F - M - S - M - M - S - M - F - M - S - M - M - S - M - M - S - M.

The subjective perception of this presentation consisted of moving black and white grains interrupted by the fixation cross/bar.

MR Image Acquisition

All measurements were performed on a 3T Philips Intera whole body system. However, experiments 1 and 2 were performed with the "Master" gradient system (30 mT/m gradient strength, 150 mT/m/ms slew rate), while experiment 3 was performed with the "Triade" gradient system (80 mT/m gradient strength, 100 mT/m/ms slew rate). The latter allows for faster data acquisition and therefore enhanced gradient-echo EPI quality in terms of susceptibility artifact reduction and reduced T2*-blurring.

Parameters of Experiment 1

Functional T2*-weighted images were acquired with an echo-planar pulse sequence (EPI) from 32 axial slices covering the whole brain with an acquisition matrix of 80 × 80 (voxel size, 2.6 × 2.6 × 4 mm^3) which was reconstructed into an image matrix of 128 × 128 (voxel size, 1.6 × 1.6 × 4 mm^3). Acquisition parameters were: TR = 4500 ms; flip angle, 90°; TE = 30 ms; and no interslice gaps.

Parameters of Experiments 2 and 3

We applied the fast imaging technique Sensitivity Encoding (SENSE) (Pruessmann et al., 1999; Weiger et al., 2000) in the second and third experiment using a transmit-receive body coil and a commercial eight-element head coil array (MRI Devices Corporation, Waukesha, WI). Parallel imaging techniques, such as SENSE, provide faster encoding by using spatially varying coil sensitivity profiles for image reconstruction. This allows the reconstruction of undersampled data. For a given spatial resolution, susceptibility-related artifacts like image distortion and blurring can be reduced by shortening the required echo train length (Preibisch et al., 2003; Schmidt et al., 2005). Functional T2*-weighted images were acquired from 32 axial slices covering the whole brain with an acquisition matrix of 80 × 80 (voxel size, 2.8 × 2.8 × 4 mm^3), which was reconstructed into an image matrix of 128 × 128 (voxel size, 1.7 × 1.7 × 4 mm^3). A SENSE single-shot-echo-planar-imaging (SENSE-sshEPI) readout was applied with a reduction factor of 2.4. Further acquisition parameters were: TR = 3000 ms; flip angle, 82°; TE = 35 ms; and no interslice gaps.

MR Image Analysis

Image postprocessing and the statistical analyses of all fMRI data were performed using Statistical Parametric Mapping (SPM2; http://www.fil.ion.ucl.ac.uk/spm/). Volumes were realigned to the first volume to remove movement-related variance components (Friston et al., 1995). As a prerequisite for intersubject averaging, images from all subjects were spatially normalized into standard stereotaxic space (standard EPI template, SPM2). Data were smoothed to a full width of 8 mm at half-maximal resolution using a Gaussian filter to increase signal-to-noise ratio and to conform data to a Gaussian field model.

The fMRI data of all subjects were analyzed voxel by voxel by modeling the conditions as boxcar functions convolved with a hemodynamic response function and applying the general linear model (fixed effects model; Cohen, 1997) provided in SPM2 (http://www.fil.ion.ucl.ac.uk/spm/). A high-pass filter with a cutoff period of 128 s was used. The six head movement parameters were included as confounding factors. We computed implicit encoding contrasts (implicit experimental encoding condition versus implicit neutral encoding condition) and explicit encoding contrasts (explicit experimental encoding condition versus explicit neutral encoding condition). The resulting within-subject contrasts of each subject were further analyzed in a second-level analysis (SPM2; random effects analysis) to account for the variance between subjects. We computed correlations between the within-subject implicit encoding contrasts and the behavioral measure of the later retrieval impairment as well as the behavioral measure of the explicit encoding facilitation (simple regression, SPM2). The retrieval impairment was expressed as % correct professional categories in the neutral condition minus % correct professional categories in the experimental condition. The explicit encoding facilitation was expressed as % (easily) imagined scenes in the experimental condition minus % (easily) imagined scenes in the neutral condition. All results were considered reliable if they exceeded a threshold of $p < 0.001$ (uncorrected); results at the lower significance level of $p < 0.01$ were only mentioned if located in the region of interest, the medial temporal lobe.

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